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NOTES ON SOME SLAVE-RAIDS OF THE WESTERN  
AMAZON ANT (*Polyergus breviceps*  
EMERY).<sup>1</sup>

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While camping during the summer of 1915 at Fallen Leaf Lake near Lake Tahoe, in the Sierras of California, I had an opportunity to observe several slave-raids of the western amazon ant (*Polyergus rufescens* Latr. subsp. *breviceps* Emery), a form not hitherto known to occur in California. In my book on the ants<sup>2</sup> I described a few forays of this ant in Colorado, but the Californian colonies exhibited some peculiarities of behavior not heretofore observed in any of our North American amazons. Only five colonies were seen during ten days devoted to the study of the ants of the Lake Tahoe region, so that in this locality *P. breviceps* is evidently much rarer than in certain localities (*e. g.*, Florissant) at the same or greater elevations in the Rocky Mountains of Colorado. The slave in all the colonies was an ill-defined variety of *Formica fusca*, less pubescent than var. *subsericea* Say or *argentea* Wheeler and larger and less shining than the typical form of the species.

The notes taken on the following dates refer to as many different colonies:

<sup>1</sup> Contributions from the Entomological Laboratory of the Bussey Institution, Harvard University, No. 113.

<sup>2</sup> Ants, Their Structure, Development and Behavior. Columbia Univ. Press, 1910, p. 475-477.

July 22. At 4.30 P. M. a large army of *breviceps* workers was seen hastening along the rocky trail, at an altitude of about 6,000 ft., on the eastern slope of Mt. Tallac, about 50 feet above the surface of Fallen Leaf Lake. The ants were followed to a *fusca* nest which they had just reached. The *fusca* workers had retired into their galleries and could be seen hurriedly closing the small entrance from within with pellets of earth, evidently for the purpose of shutting the amazons out. The latter, however, at once tore out the barricade and poured into the nest. Soon they began to bring up the *fusca* pupæ and at once hurried back over the trail. I followed them to their own nest which was nearly 60 feet from the plundered colony, in the narrow crevices of some large rocks where it could not be examined. By 5.15 P. M. all the amazons had entered their nest. The supply of *fusca* brood secured on this raid was not considerable, since only about one in ten of the returning workers carried a pupa or larva in its jaws. Retracing my steps to the *fusca* nest, I found its inhabitants slowly and apparently with reluctance returning to it.

July 24. A small colony consisting of a wingless, ergatoid female and about a dozen small *breviceps* workers and nearly two dozen *fusca* workers was found under a log in a warm hollow at an altitude of nearly 7,000 ft. on the eastern slope of Angora Peak. This was evidently a young colony, with the ergatoid female functioning as its queen. This insect had the gaster considerably distended with eggs.

July 25. At 4.20 P. M. I encountered a small colony of *breviceps* returning from a raid on the Mt. Tallac trail near Fallen Leaf Lodge, not far from the spot where I observed the foray of July 22. I did not stop to locate the nest.

July 29. At 3.45 P. M. I came upon a large *breviceps* army returning to its nest laden with pupæ near Glen Alpine Springs at an altitude of about 7,000 ft. The nest was easily found under a large flat stone, which I lifted just before the returning army arrived. The nest-chambers were full of *fusca* workers and pupæ, but only two or three amazons had remained among them, and had not, therefore, taken part in the foray.

The notes taken on the following dates refer to a single *breviceps* colony which was observed on five consecutive days, not only by myself but also by many of my fellow campers and by Mr. Wm. W.

Price, the genial ornithologist and proprietor of Fallen Leaf Lodge:

July 26. At 4.10 P. M. I discovered the nest of a very large *breviceps* colony under a small flat stone near the mouth of the canyon through which the stream runs from Glen Alpine Springs to Fallen Leaf Lake. The army of several hundred workers was just emerging and congregating around the three nest orifices in preparation for a foray. The ants very soon hurried off in great excitement down the canyon to a *fusca* nest at least 70 feet distant. The trail was difficult, as the insects had to cross a very dusty road, climb over a pile of rough boulders, creep under a lot of low bushes and then traverse many feet of rocky soil. The first individuals, however, reached the *fusca* nest at 4.30 P. M. and at once entered it through several openings so small and so much obstructed with pellets of earth that I should not have found the nest without the guidance of the amazons. The *fusca* workers offered no resistance, but fled in all directions. A few managed to escape with larvæ in their jaws. The amazons poured into the nest entrances and soon emerged with the first pupæ, nearly all of which were naked (*i. e.*, not enclosed in cocoons) at 4.40 P. M. and at once started for home. The vanguard of the returning army, nearly every worker of which was carrying a pupa, reached the nest at 4.55 P. M. and the last stragglers had arrived by 5.10 P. M. The foray was therefore completed in an hour. It was accompanied by an unusual performance—a partial marriage flight. About 20 winged female amazons and a greater number of males left the nest with the army of workers and while some of the couples lingered behind and mated on the ground or low vegetation and several of the males flew away without mating with their sisters, several of the females accompanied the workers and even entered the *fusca* nest. None, however, was seen to return with the pupa-laden workers. A few, which had mated, tore off their wings and ran about over the ground. They probably returned to the nest after I had left the spot.

July 27. I visited the amazon nest at 3.35 P. M. and found that the army had just departed. It took a more northerly direction than on the preceding day, and after covering a distance of about 75 feet, stopped and began to hunt about among the stones and sparse vegetation. After several minutes devoted to this search, the greater portion of the army moved on but the remainder discovered a small

*fusca* nest, plundered it without opposition and at once returned home with all the pupæ that could be secured. The main army hurried on over a very rough, stony trail. They stopped twice, searched about diligently but in vain, and each time changed the direction of their route. Several completely or partially deälated females accompanied the main army the whole distance and seemed to be quite as keenly interested in the proceedings as the workers. The army halted a third time at a spot 125 feet distant from the point where the first nest was plundered and succeeded in discovering a flourishing *fusca* colony consisting of large workers. These were very aggressive and fully prepared to defend their nest, which, like all the *fusca* nests in the vicinity of the amazon colony, was very carefully concealed under and between stones. The amazons reached this nest at 4.30 P. M. and exhibited great excitement. Some of them attacked the *fusca* fiercely, while others kept digging their way into the earth-barricaded entrances. *Fusca* workers could be seen defending their doorways from within, but they were mercilessly dragged out and massacred in the usual manner, by having their heads pierced with the sickle-shaped mandibles of the amazons. Finally, after a struggle of fully 30 minutes, at 5 P. M. the first *fusca* pupæ were brought out. Their bearers turned at once in the direction of their nest, nearly 200 feet away and hurried towards it over a path, *which, for fully 40 feet, was entirely different from the one over which they had come.* A stream of pupa-laden amazons issued from each of two nest orifices and at once united to form a single file. Even the young callow *fusca* workers were dragged out by the antennæ and then seized by the thorax and carried along. Several of the deälated females returned with the workers but none was seen to carry a pupa. The army reached the home nest at 5.30 P. M., so that this foray, during which two *fusca* colonies had been thoroughly plundered, and fully 400 feet of ground had been traversed by most of the individuals, was completed in two hours.

July 28. The amazon army left the nest at 4.15 P. M., plundered a large *fusca* colony after traversing nearly 80 feet of rough, stony soil to the southeastward, and returned with many pupæ by 5.30 P. M. The army was accompanied both to and from the *fusca* nest by several deälated females, but none of them carried pupæ.

July 29. I arrived late at the amazon nest, but found Mr. Price

already there with several campers, all intently watching the ants. According to their statements, the army left the nest about 3 P. M. After going some 60 ft. it hesitated and part of it discovered a small *fusca* colony, plundered it and returned home at once with the booty, while about half of the army changed its direction and proceeded to a point about 80 feet from the home nest in a more northerly direction than any of the previous forays and along the bank of the stream. The ants soon succeeded in detecting a *fusca* colony, which, however, offered stubborn resistance. This was overcome and the robbers were all returning laden with pupæ when I reached the spot between 4.50 and 5 P. M. One of the observers saw a few winged amazon females in the outward-bound army, but none was seen returning to the nest.

July 30. The amazon nest was watched by Mr. Price, about twenty campers and myself from 2.30 to 4.30 P. M. but made no foray. This was very probably due to the weather, which was cloudy and much colder than on the preceding days. Nevertheless quite a number of males escaped from the nest, especially between 2.30 and 3.30 P. M. Some of them flew away, others almost immediately returned to the nest and several were violently dragged back into it by the *fusca* slaves. Only two deälated females left the nest. They ran about for some time and then returned into the entrances of their own accord. The slaves were very active at all three entrances and seemed to be constantly keeping the worker amazons from making a sortie. On lifting the stone covering the galleries several winged females were seen near one of the entrances, but none of them left the nest. The following morning I was compelled to leave Fallen Leaf Lodge and was therefore unable to continue my observations.

The following points are particularly interesting in these field observations in connection with those recorded in my ant book on the same subspecies in Colorado, *P. rufescens bicolor* in Illinois and *P. lucidus* in New York:

1. Although it is known that both the European and American amazons make their raids only during the afternoon, the sorties previously recorded for our American forms, though also observed during July, occurred at an earlier hour, as follows: *brevicaps* at 1.55 P. M. *bicolor* before 2 P. M.; at 1.35 and 1.20 P. M.; *lucidus* at 2.20 P. M. One foray of *lucidus* observed by Burrill in Pennsylvania started be-

fore 2.30 P. M.<sup>3</sup> The four sorties of *breviceps* observed near Fallen Leaf Lake occurred at 4.10, 3.35, 4.15 and 3 P. M., and the three armies merely seen returning to the nest July 22, 25 and 29, could hardly have started out before 3 P. M. In this connection I may mention, also, that the two forays of the small shining *P. rufescens laviceps* Wheeler which I observed July 20, 1914, on the slopes of Mt. Tamalpais, near San Francisco, Calif., must have left their nests after 3 P. M. How are we to account for this difference in time of sortie between the Californian amazons and those of Colorado, Illinois, Pennsylvania and New York?

Before attempting to answer this question it will be advisable to glance at some of the published accounts of the typical European *P. rufescens*. The most comprehensive observations on this ant have been made by Forel in Switzerland.<sup>4</sup> During 33 days he saw a single *rufescens* colony make 44 expeditions and estimated that the ants secured from the various plundered colonies of *F. fusca* and *rufibarbis*, on these and other expeditions, which he did not observe, a total of fully 40,000 larvæ and pupæ. Concerning the time of sortie in general he writes (p. 289): "As Huber says, *P. rufescens* nearly always leaves its nest in the afternoon between 2 and 5 o'clock. Von Hagens saw a sortie at 6 P. M.; I have observed two at 1.30 P. M. These are, to my knowledge, the extreme cases. Expeditions have never been observed in the morning. Ebrard says that they depart very late on their first expedition (during June) and thereafter a little earlier each day. I have never observed anything of the kind. I have seen amazons from two different formicaries departing at 2.15 P. M. and at 4 P. M. respectively. On the other hand I have seen amazons of the same colony depart on several successive raids at the same hour. The hour of departure depends as a rule on the temperature; the warmer it is, the later do the amazons depart and *vice versa*. The amazons of the same formicary departed during one year as follows: July 1, 3.15 P. M.; July 23, 5 P. M.; Aug. 10, 3 P. M.; Aug. 12, 1.30 P. M.; Aug. 14, 4.45 P. M., etc. The departure of Aug. 10 and 12 coincided with a pronounced and sudden drop, that of Aug. 14 with a pronounced rise of temperature. According to the formicaries, the

<sup>3</sup> "A Slave-making Foray of the Shining Amazon (*Polyergus lucidus* Mayr)," JOURN. N. Y. ENT. SOC., 16, 1908, pp. 144-151.

<sup>4</sup> Fourmis da la Suisse, 1874.

expeditions begin from the middle of June to the beginning of July (possibly sooner in very warm localities) and end between the middle of August and beginning of the September." Emery,<sup>5</sup> who has succeeded in solving the interesting problem of the establishment of amazon colonies, gives the time of two forays of a colony in northern Italy during 1908 as July 24, 4.30 P. M. and July 25, 3 P. M. and of two forays of this same colony during 1907 as July 16, 4.30 to 5 P. M. and July 19, as 5 to 7 P. M.

Forel is probably correct in supposing that the time of sortie of the amazon army is determined by temperature. We may suppose that a certain optimum, probably near 70° to 75° F., is required by the ants. This is often attained during the sunny afternoon hours of July and August in temperate North America and Eurasia. It would certainly be below the usual maximum diurnal temperature and would bear a certain relation to it, so that it would be reached earlier in the afternoon on hot than on cool days. Thus we could account for the differences in the time of sortie between the Californian amazon colonies and those of the Rocky Mountains, Middle and Eastern States since the average midday temperatures of July at altitudes of 6,000 to 8,000 ft., on the southern and eastern slopes and in the canyons preferred by the ants, is certainly much lower in California than it is in the other localities mentioned. It is not improbable, however, that atmospheric humidity may also be a factor in determining the time of sortie. At any rate, all future descriptions of amazon expeditions, both in this country and abroad, should be accompanied by accurate temperature, barometric and humidity records, for in time such records might enable us to ascertain the precise external stimuli that call forth such periodic behavior as the slave-raids and nuptial flights of ants.

2. The second matter of interest in the observations made at Fallen Leaf Lake is the behavior of the males and females of *breviceps*. Emery has been puzzled by the behavior of these forms in the European *rufescens*. Huber and Forel had witnessed marriage flights of this ant and Burrell<sup>6</sup> described a feeble marriage flight of

<sup>5</sup> Osservazioni ed Esperimenti sulla Formica Amazzone. Rend. Sess. R. Accad. Sci. Ist. Bologna, 1908, 16 pp.; Nuove Osservazioni ed Esperimenti sulla Formica Amazzone, *ibid.*, 1909, 8 pp.; Ulteriori Osservazioni ed Esperimenti sulla Formica Amazzone, *ibid.*, 1911, 18 pp.

<sup>6</sup> *Loco citato*, p. 150.

*lucidus* July 22, 1903. Aug. 20, 1903, I saw a large and very typical flight of *lucidus* subsp. *montivagus* Wheeler near Colorado Springs. Emery observed a colony of *rufescens*, which, during 1907, had no marriage flight but from which winged and deãlated females issued and accompanied the workers on their forays. In 1908 the same colony gave off a lot of males which flew away but no females accompanied the raids. The observations on the Californian *breviceps* show that the males and females may stay long in the maternal nest, that some of them may escape from time to time and mate outside the nest and that both winged and fecundated, deãlated females may accompany the workers on their raids while a marriage-flight is taking place. A single colony may thus exhibit during the course of a few days combinations of the two extreme conditions noticed by Emery during two seasons. I called attention to the protracted retention in the nest of males and females of *lucidus* in 1908,<sup>7</sup> but before making the observations on the Californian *breviceps* I had never seen the females accompanying the workers on their raids, though both Emery and Forel had seen this repeatedly in the typical *rufescens*. These authors have also failed to notice any inclination on the part of the females to bring home pupæ. My observations leave me skeptical in regard to Emery's assumption that the female *Polyergus* mates inside the nest.

Emery's observations on colonies kept in artificial nests show conclusively that the fecundated and deãlated female of *Polyergus* founds her colony by entering a *fusca* formicary, killing its queen by piercing her head with the mandibles and securing adoption in her place by the *fusca* workers. Does the female, while accompanying the foraging army, gain acquaintance with the situations and personnel of the various *fusca* nests in the area dominated by the *Polyergus* colony, so that she can at her leisure select and invade a propitious colony in which to secure adoption? Or does she actually secure adoption in a colony which has just been plundered and is therefore in a depressed and nonresistant state, as seems always to be the case with *fusca* colonies after they have had to submit to this sudden and severe calamity? The former method is suggested by the iso-

<sup>7</sup> "The Ants of Casco Bay, Maine, with Observations on Two Races of *Formica sanguinea* Latreille," Bull. Amer. Mus. Nat. Hist., 24, 1908, p. 640 nota.

lated deälated females sometimes found running about on the ground at a distance from the maternal nest, as if looking for a host-colony; the latter method would seem to have many advantages. Perhaps both methods are adopted by different females.

3. The finding on July 24 (p. 108) of a small and evidently incipient *breviceps* colony consisting of an ergatoid or wingless female with about a dozen workers and twice as many *fusca* slaves, is significant, because the female was functioning as the mother of the colony and must therefore have been fecundated. The ergatoid female of the European amazon has been known for more than a century. It was first recognized by Pierre Huber<sup>8</sup> and has been repeatedly taken by Forel, Emery and Wasmann. According to Forel (*Fourmis de la Suisse*, p. 137), "this singular creature, which is very constant in type, is rather rare. Nevertheless, during certain years some specimens of it are found in most of the formicaries. Its rôle, if it has one, is unknown. Perhaps it can replace the queens in their functions. Dissection has proved to me that its ovaries are identical with those of the queen, etc." Wasmann<sup>9</sup> describes one of these females which he kept in an artificial nest with amazon workers and slaves from April, 1885, to September, 1886. It was treated by the slaves as a true queen, licked, fed and, when disturbed, carried to a place of safety. Its eggs, however, produced only males, showing that it had not been fecundated. In 1908 I published a similar observation<sup>10</sup> on a large colony of *lucidus* which I had under observation for five years in a field near Bronxville, N. Y.: "During four years this colony produced numbers of males and females, both winged and ergatoid, and the winged females lingered for weeks in the nest without deälation. The first week of the past April [1908] I found the whole community with its larvæ and mother queen enjoying the spring warmth in the superficial galleries just under the large flat stones with which I had covered the nest in September, 1903. I captured the queen and part of the colony and transferred them to an artificial nest. Aug. 9 [1908] I again visited the nest, and to my surprise, found it teeming with several hundred mature males clinging to the

<sup>8</sup> Recherches sur les Mœurs des Fourmis Indigènes. 1810, p. 251.

<sup>9</sup> Die zusammengesetzten Nester und gemischten Kolonien der Ameisen, Münster s.W., 1891, p. 84.

<sup>10</sup> Ants of Casco Bay, etc., *loc. cit.*, p. 141, *nota*.

lower surface of the stone, but with no winged or deãlated females. Besides the males I found only a single large ergatoid female, several dozen workers and slaves [*Formica incerta*] and half a dozen cocoons enclosing nearly mature male pupæ. Without doubt, the ergatoid had usurped the rôle of the mother queen, and being unfertilized, had produced only male offspring. The comparatively small number of slaves had been able to rear an enormous number of these little creatures although the absence of *incerta* pupæ in the nest indicated that the *Polyergus* workers had made no forays during the past summer." Emery<sup>11</sup> cites an unpublished observation of Wasmann concerning an ergatoid female of *rufescens* which produced workers and must therefore have been fecundated. This observation supports my interpretation of the origin of the *breviceps* colony taken on Angora Peak, Cal., July 24. Emery believes that the ergatoid females may be fecundated in the maternal nest, but this might occur quite as easily outside the nest and on the ground during a marriage flight of the males.

Considerable interest attaches to the ergatoid female of *Polyergus* because it is so much like the only females known to occur in certain tropical ant genera such as *Leptogenys*, *Onychomyrmex* and *Paranomopone*. It suggests that the ants of these genera once possessed, like *Polyergus*, two kinds of females, one winged and one wingless, and that the colonies for some reason no longer develop the former. In the singular parasitic *Hapagoxenus sublaevis* the two forms still occur but in different geographical regions, the winged form in Saxony, as Viehmeyer has shown, and the wingless form in Sweden, as was first established by the classical observations of Adlerz.

#### POSTSCRIPT.

After the preceding pages were written I received a fourth interesting paper from Professor Emery on the amazon colony which he had under observation from 1908 to 1914.<sup>12</sup> In 1908 and 1909 he succeeded in establishing in artificial nests two amazon colonies with the aid of two fecundated queens that had secured adoption by *fusca* workers. In March 1910, he combined the two formicaries and the

<sup>11</sup> Osservazioni e Esperimenti, etc., 1908, *loc. cit.*, p. 7.

<sup>12</sup> Histoire d'une Société Expérimentale de *Polyergus rufescens*, Rev. Suisse Zool., 23, 1915, pp. 285-400, 2 figs.

single colony thus formed flourished and grew to considerable size by July 18, 1911, when he took it into his garden and observed the behavior of the amazons when he opened the nest and permitted them to make slave-raids on various colonies of *Formica fusca* var. *glebaria* and *F. rufibarbis*. Similar experiments were performed during the summer of 1912 and 1913. July 14, 1914, when he released the colony for the last time in a courtyard of his villa, the ants established themselves in the soil and soon afterwards moved to another more permanent nest. The amazons made several sorties till October 2, but secured no booty, as there were no nests of the slave-species in the courtyard. The observations were very suggestive in connection with the interesting problem as to how the amazon armies are guided to the nests they plunder. Like Forel and myself, Emery believes that exploring workers, which leave the nest singly, ascertain the position of the slave colonies in the environment and are thus able to determine at least the initial direction to be taken by the army when it leaves the nest. I shall not discuss this difficult question here, but will merely call attention in conclusion to the times of sortie of the army as recorded in Emery's paper. These are given as follows:

1911.	Aug.	22—4.30	P. M. and 5.15 P. M.
1912.	"	17—5.00	P. M. and 6.30 P. M.
	"	21—4.20	P. M.
	"	24—4.30	P. M.
	"	28—5.40	P. M.
1913.	July	5—4.50	P. M.
	"	30—5.15	P. M.
1914.	"	16—6.00	P. M.
	"	17—6.30	P. M.
	"	25—7.00	P. M.
	Aug.	8—5.30	P. M. and 6.15 P. M.
	Oct.	2—3.30	P. M.

It will be seen that all but one of the sorties were very late, between 4.20 and 7 P. M., the average time being about 5.30 P. M. This is much later than the average time of sortie of Swiss colonies of *rufescens* or of the Californian *breviceps*, and indicates that the temperature during July and August in northern Italy (presumably near Bologna), in such enclosed spaces as gardens and courtyards, may be

higher in the late afternoon. On Aug. 22, 1911, Aug. 12, 1912, and Aug. 16, 1914, two sorties occurred on the same day. This has also been occasionally observed by Forel in the field. On Aug. 9, 1914, there were three sorties, but the time of their occurrence was not recorded.

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## NEW LIMNOPHILINE CRANE-FLIES FROM THE UNITED STATES AND CANADA (TIPULIDÆ, DIPTERA).

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The tribe Limnophilini of the subfamily Limnobiinæ, in the Nearctic fauna, includes a considerable number of species placed in a relatively small number of genera. During the past few years a number of interesting forms have accumulated in the collection of the author and these are described herewith; I am greatly indebted to Mr. C. W. Johnson, Mr. Frederick Knab and Mr. W. L. McAtee for the loan of this and other material sent me for study.

### ***Limnophila marchandi*, new species.**

Allied to *L. alleni*; color of the thorax gray; ground color of the wings hyaline; basal abdominal tergites gray with prominent setigerous punctures.

Female.—Length, 30 mm.; wing, 20 mm.; Middle leg, femora, 10 mm.; tibiæ, 8.7 mm.; tarsi, 8.6 mm.

Rostrum short, dark brown, palpi dark brown. Antennæ with the two basal segments dark brown, the flagellum light brown; first scapal segment elongated; segments of the flagellum short, gradually narrowed to the seventh segment of the organ beyond which the segments are very slender and attenuated. Head dark brown, the margin of the vertex adjoining the inner margin of the eye, paler, more yellowish; head narrowed behind.

Pronotum light brownish gray, clearer gray on the sides, with a delicate impressed median line; scutum with numerous long hairs whose bases are surrounded by brown spots. Mesonotal præscutum clear light gray with three dark brown stripes; the middle stripe is broad, the median area is paler brown and narrowly bisected by a very delicate dark brown median line which runs the length of the sclerite; the middle stripe does not attain the transverse suture; lateral stripes short, crossing the transverse suture onto the scutum; the pale area between the lateral and middle stripes is lined with a paler shade of brown; sides of the sclerite bearing abundant long pale